

Periods of dormancy and cohort-splitting in the millipede *Polydesmus angustus* (Diplopoda: Polydesmidae)

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Abstract. First stadium juveniles of *P. angustus* were reared under controlled seasonal conditions to maturity, reproduction and death. Individuals born in any one breeding season either had a 1-year or a 2-year life cycle (cohort-splitting). The life cycle was annual for individuals born in the first part of the breeding season (May–August), but became biennial for those born later (August–October). Two phenomena were involved: (1) Only individuals reaching the penultimate stadium (stadium VII) before a critical period at the end of spring could become adult in the breeding season following that of their birth. After this time, stadium VII individuals entered into aestivation and only became adult in the second autumn after their birth. (2) Females becoming adult in autumn entered reproductive dormancy and only laid eggs in the following spring. Overall, individuals born at the start of the breeding season easily reached stadium VII before the critical period and were able to breed at 1 year, whereas individuals born at the end of the breeding season reached stadium VII after the critical period, then had two consecutive periods of dormancy and only bred at 2 years age. Individuals from the same nest born in the middle of the breeding season (August) could have either annual or biennial life cycles, depending on whether they reached stadium VII before or during aestivation. The environmental factors capable of triggering aestivation in subadults and reproductive dormancy in autumn-maturing females are discussed.

INTRODUCTION

In a field population of the woodlouse *Philoscia muscorum* (Scopoli) (Isopoda: Oniscidae), Sunderland et al. (1976) observed that individuals born in one breeding season split into two groups differing in speed of growth, the “fast group” breeding the following year and the “slow group” two years after birth. They called this phenomenon cohort-splitting. Willows (1987) proposed the term year-class splitting, but if a cohort is defined as the members of a population born in the same season (Stearns, 1992) the original term can be retained. Similar phenomena have been observed in other species of soil arthropods, such as the woodlouse *Trichoniscus pusillus* Brandt (Isopoda: Trichoniscidae) (Phillipson, 1983), the millipedes *Polydesmus inconstans* Latzel and *Polydesmus angustus* Latzel (Polydesmida: Polydesmidae) (Snider, 1984; David et al., 1993) and the crane fly *Tipula montana* Curtis (Diptera: Tipulidae) (Todd, 1996).

Cohort-splitting is of interest in studies of population dynamics and life-history evolution, provided the causes of variation in the life cycle of each species are known. These cannot be identified by sampling populations in the field and laboratory investigations are needed. In *P. muscorum*, Grundy & Sutton (1989) showed that populations maintained under constant laboratory conditions did not develop cohort-splitting, but that populations reared outdoors – or with seasonal changes in temperature and day-length simulated in the laboratory – were clearly divided into two groups with different growth rates. Grundy & Sutton (1989) also showed that the fast-growing individuals were almost entirely from the first broods, whereas the

slow-growing individuals came from second broods produced about 5 weeks later than the first in *P. muscorum*. These authors attributed the growth retardation of late recruits to stress encountered during their first winter, because of their smaller body size. However, the reared animals were only studied for a year and complete life cycles of 2 years were never observed.

In *P. angustus*, preliminary studies over a period of one year also left a number of questions unanswered (David et al., 1993). We have now monitored complete cycles in the laboratory – from hatching to maturity, reproduction and death – in a number of individuals with 1-year and 2-year life cycles. Our observations first of all show that cohort-splitting is an established phenomenon in a seasonal environment. They also make it possible to compare the calendar of development and reproduction between the two life cycles, thus demonstrating that periods of dormancy are responsible for the prolonged cycle in some individuals. This is the subject of the present paper – the first stage in an ecophysiological approach that will be followed later by further experimental studies.

MATERIAL AND METHODS

The saprophagous millipede *P. angustus* is very common in forest soils of north-western Europe. The present study was conducted on animals originating from Brunoy (France), 20 km south-east of Paris. The post-embryonic development of the species is well-known and invariably consists of eight stadia (=instars), the last of which is the adult. Individuals can be assigned to a stadium by counting the number of body rings and sexed from stadium IV onwards (Blower, 1985). Polydesmid females lay eggs in nests that are easy to find in cultures, and the young leave the nest soon after hatching (Stephenson, 1961; Snider

1981a, b). In *P. angustus*, the reproductive period extends over several months, from spring to early autumn, both in the field and in the laboratory (Sahli, 1969; Banerjee, 1973; David et al., 1993). This is because females start laying at different times and each female can produce up to four or five nests, at several weeks' interval, before dying (David & Célérier, 1993; David et al., 1993).

Life-cycle studies in laboratory cultures

Stadium I individuals were obtained in the laboratory from mated females originating either from the field or from previous cultures (first and second generations under laboratory conditions). First stadia born at different dates were transferred with a brush to transparent, lidded plastic boxes (400 ml), containing about 1 cm soil sieved to 2 mm. The young from any one nest were kept in groups for the first few months, and were then isolated in ones or twos per box so as to monitor their life cycles individually. The millipedes were fed continually with leaf litter rinsed in distilled water and received a pinch of dry food yeast (*Saccharomyces cerevisiae*) each month, this being essential to obtain adult live weights and fertility close to those in the field (David & Célérier, 1997). Cultures were conducted in a periodic environment close to natural conditions using a controlled-temperature cabinet fitted with a glass door. The natural photoperiod was unchanged and temperature followed the mean monthly temperatures of the region of origin, with a daily thermoperiod (12C : 12T) of 4°C amplitude (or 2°C in the three coldest months) (Table 1). The soil and litter were kept moist throughout the year. Cultures were started with the photoperiod of Brunoy (48°42'N), then animals were transported further south to Montpellier (43°36'N), for convenience. The soil, food and temperature were the same as at Brunoy; only the natural photoperiod changed.

TABLE 1. Monthly temperatures at which *Polydesmus angustus* was reared during the study.

	Day T (°C) (12 h)	Night T (°C) (12 h)	Mean T (°C)
January	4	2	3
February	5	3	4
March	9	5	7
April	11	7	9
May	15	11	13
June	18	14	16
July	20	16	18
August	20	16	18
September	18	14	16
October	14	10	12
November	9	5	7
December	5	3	4

The birthday of an individual was its first observation at stadium I and other events in the life cycle (emergence of a stadium or of the adult, egg-laying, hatching, death) were also dated to the first day of their observation. As boxes were observed from 1 to 3 times per week, the possible error in dating the birthday – and in estimating the time elapsed between birth and the other events – was between 0 and 7 days (most often between 0 and 4 days). Data were converted into months on the basis of 30.4 days per month and differences were tested using the Mann-Whitney U-test with correction for ties (t_s -statistic; Sokal & Rohlf, 1995).

Effect of a change in temperature regime

Thirty-six individuals born in late August and September in four different nests were divided into two groups on 1 Novem-

ber – each group receiving half of the individuals from each nest. The first group was reared at the monthly temperatures shown in Table 1 and the second at temperatures increased by 4°C from November to April – except in January when the mean temperature was maintained at $3 \pm 1^\circ\text{C}$. The numbers of individuals in each stadium, which were the same in both groups on 1 November, were recorded at regular intervals until all individuals reached maturity (stadium VIII). The effect of the two temperature regimes on the proportions of stadia was tested using the G-test with Williams' correction (Ga-statistic; Sokal & Rohlf, 1995).

RESULTS

The two life cycles

There was a distinct breeding season in our cultures. Laboratory-reared females laid eggs over a period of 6.2 months, from 20 March to 23 September. The breeding season proper, i.e. the period of recruitment, was however slightly shorter (5.4 months, from 7 May to 17 October), because the development of eggs was faster at the end of the season than at the beginning (24 days for the last nests in September–October compared to 48 days for the first nests from March to May).

Fifty-two females were individually monitored from birth to reproduction and death. Forty of these bred in the breeding season following that of their birth. They started breeding at the age of 12.0 ± 0.1 months (mean \pm SE) (range 11.1–14.1), and they survived for 14.9 ± 0.4 months (range 11.2–21.1). These females represent the 1-year life cycle. The other twelve bred in the second breeding season after that of their birth. They started breeding at the age of 20.6 ± 0.2 months (range 19.6–21.2) and survived for 22.8 ± 0.1 months (range 22.5–23.6). These females represent the 2-year life cycle. No female bred in two consecutive seasons.

Cohort-splitting also occurred in males. Although their breeding period was more difficult to identify, they could also be divided into two groups. Forty-four males became adult early enough to have offspring in the first breeding season after that of their birth. These males survived for 15.3 ± 0.7 months (range 12.0–23.0), which was not significantly different from the survival of annual females ($t_s = 0.03$; $P > 0.90$). Another group of 15 males reached the adult stage later (see below) and could only produce offspring in the second breeding season after that of their birth. This second group survived for 22.7 ± 0.3 months (range 20.4–23.9), which was not significantly different from the survival of biennial females ($t_s = 0.04$; $P > 0.90$). By analogy these two groups can be considered to be annual and biennial males, respectively – but it is likely that some "annual" males could breed in two consecutive seasons.

Life-cycle variation in relation to hatching date

We reared individuals of both sexes born in each month from May to October. The time taken to reach maturity was very variable (Fig. 1 for females). A small proportion of individuals born in May and June became adult in the first autumn after their birth, at the age of 4.7 ± 0.2 months in males and 5.2 ± 0.3 months in females (Fig. 1a). All the other individuals spent their first winter in an

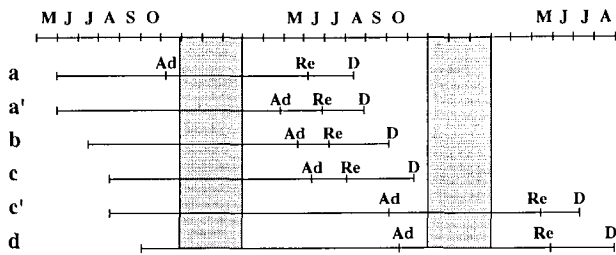


Fig. 1. Life-cycle variation in relation to hatching date in laboratory-reared females of *Polydesmus angustus*. a & a': hatching in May–June; b: hatching in July; c & c': hatching in August; d: hatching in September–October. The mean dates for adult emergence (Ad), start of recruitment (Re) and death (D) are shown for each life cycle. The winter months are shown in grey.

immature stadium, ranging from stadium VII for those born in May–June to stadium III for those born in September–October. Moulting stopped in winter and resumed in spring, sometimes as early as March (mean temperature 7°C). All the individuals born from May to July and a proportion of those born in August then reached the adult stage in spring and early summer, at the age of 10.0 ± 0.2 months in males (range 8.9–11.7) and 10.3 ± 0.1 months in females (range 9.1–12.1) (Fig. 1a', b, c). The difference between sexes was significant ($t_s = 2.26$; $P < 0.05$), males maturing faster than females. The remainder of the individuals born in August and those born in September–October only reached the adult stage in the second autumn after their birth, at the age of 12.6 ± 0.2 months in males (range 11.8–13.3) and 13.3 ± 0.2 months in females (range 12.3–14.2) (Fig. 1c', d). These values were much higher than those of individuals maturing in spring and early summer, with highly significant differences in both males ($t_s = 4.40$; $P < 0.001$) and females ($t_s = 4.79$; $P < 0.001$). Here also the difference between sexes was significant ($t_s = 2.33$; $P < 0.05$), males maturing faster than females.

The time elapsed between achievement of maturity in females and production of their first offspring was also very variable. Figure 1 shows that no female maturing in autumn, whether this was at the age of 5.2 or 13.3 months, bred before winter (Fig. 1a, c', d). These females started laying eggs only from late March or early April and hatching took place in May, on average 7.2 ± 0.2 months after maturity was achieved (range 6.0–7.8). In contrast, females maturing in spring and early summer bred rapidly, on average 1.7 ± 0.1 months after maturity was achieved (range 0.9–2.4) (Fig. 1a', b, c). These differences tended to synchronize the reproduction of females that reached maturity at 5.2 months and at 10.3 months; on the other hand, they separated the reproduction of those females that reached maturity at 10.3 months and at 13.3 months by almost a year.

Overall, all the male and female individuals born before August had a 1-year life cycle, whereas all those born after August had a 2-year life cycle. Under the rearing conditions used in our study, August was the key month in which both annual and biennial individuals were produced (Fig. 1c, c'). During this month, even individuals

from the same nest could have either a 1-year or a 2-year life cycle.

Importance of stadium VII for the life-cycle duration

The comparison of annual and biennial individuals born at the same time in August (Fig. 1c, c') showed that the duration of stadium VII – the last immature stadium during which sexual development is completed – differed greatly between the two groups. This led us to re-examine the duration of stadium VII in a larger group of individuals born in August and September, and reared either in Montpellier or at Brunoy. Figure 2 shows that the duration of this stadium changed considerably depending on the date of emergence (i.e., the time when the millipede emerged from the moulting chamber as stadium VII).

In Montpellier, stadium VII lasted on average 50 ± 3 days (range 46–56) in males and 60 ± 4 days (range 53–71) in females when subadults emerged in the first week of April. The duration decreased progressively during spring for subadults emerging up to 1 June in males and 7 June in females. This resulted in adult emergences until early July. However, when stadium VII individuals emerged later in June (from 2 June onwards in males and 20 June in females), the duration of this stadium increased sharply to 99 ± 4 days (range 84–112) in males and 104 ± 1 days (range 102–104) in females. This put back the emergence of adults to beyond 12 September in

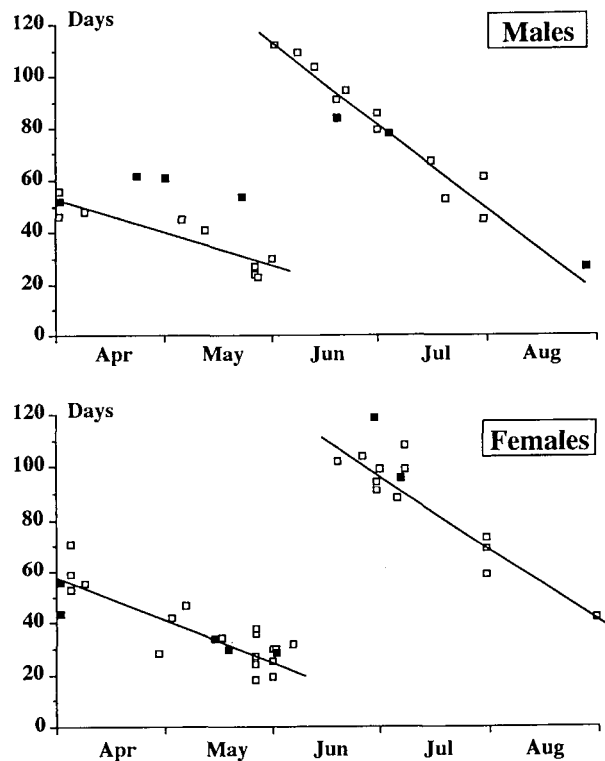


Fig. 2. Variation in the duration of stadium VII in *Polydesmus angustus* in relation to the date of emergence as stadium VII. Data from Montpellier (□) and Brunoy (■). Rearing temperatures were the same at both localities, but daylength was longer at Brunoy at this period of the year. Note the sudden increase in the duration of stadium VII for individuals emerging in June. Regression lines have been calculated before and after entry to aestivation using the data from Montpellier.

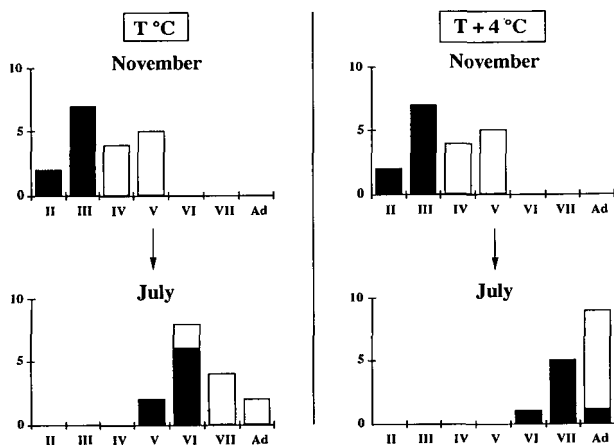


Fig. 3. Comparison of the post-embryonic development of *Polydesmus angustus* from November to July under two temperature regimes – either with a normal ($T^{\circ}\text{C}$) or a mild winter ($T + 4^{\circ}\text{C}$). Columns represent the numbers of individuals in each stadium. The stadia reached by individuals born in late August and September are shown in white and black, respectively.

males and 29 September in females. The stadium VII duration then progressively decreased when subadults emerged later in the summer, this being a powerful factor for synchronizing adult emergences in autumn (Fig. 2).

At Brunoy, there were fewer precise data on the duration of stadium VII. On the whole they showed the same pattern as in Montpellier, with a sharp increase in duration at the end of spring, followed by a progressive decrease during summer. There appears to be no difference between the two localities in terms of the period when stadium VII duration suddenly increased (Fig. 2).

The duration of the penultimate stadium in late spring-early summer was decisive for the duration of the entire life cycle, since all those individuals that reached stadium VII before its lengthening in June later had a 1-year life cycle, whereas all those that reached stadium VII after its lengthening in June had a 2-year life cycle. The first were early recruits born from May to July – that all reached stadium VII well before next June – and some of the individuals born in August that reached stadium VII before 2 June in males and 20 June in females. The individuals with a long life cycle were the remainder of those born in August, which reached stadium VII from 2 June onwards in males and 20 June in females, and late recruits born in September–October, that all reached stadium VII after the month of June.

Effect of a change in temperature regime

Stadial spectra obtained with the average temperature regime and with higher temperatures from November to April (mild winter) are shown in Fig. 3. At normal temperatures, the results expected for individuals born in late August and September were obtained. Individuals born in August had either 1-year life cycles (adults in July) or 2-year life cycles (stadia VI and VII in July); all individuals born in September had 2-year life cycles (stadia V and VI in July). Under milder winter conditions, the month in which annual and biennial individuals were produced

shifted to September: all individuals born in late August had 1-year life cycles (adults in July), whereas individuals born in September had either 1-year life cycles (one adult in July) or 2-year life cycles (stadia VI and VII in July). The proportions of the two cycles were significantly altered by the change in temperature regime ($G_a = 7.66$; $P < 0.01$) which shows that individuals that would probably have been biennial at normal temperatures became annual at higher temperatures.

All individuals that became annual at higher temperatures reached stadium VII before 3 June and stayed in this stadium for a relatively short time (mean duration 52 ± 7 days). In contrast, all individuals that remained biennial at higher temperatures reached stadium VII after 27 June and stayed in this stadium for a much longer time (mean duration 98 ± 3 days). It was therefore in June that there was a critical period for the split in the cohort – exactly as for individuals reared at normal temperatures.

DISCUSSION

In a seasonal environment closely simulating natural conditions, it is possible to recreate cohort-splitting in a laboratory population of *P. angustus*. Females born in one breeding season, from May to October, reproduce either in the following breeding season (when about 1-year old), or in the second breeding season after that of their birth (when nearly 2-years old). One-year life cycles occur in females that hatch early in the season (May to August under the conditions used in this study), and 2-year life cycles in females hatching later (August to October under the same conditions). The pattern is almost the same in males.

Sunderland et al. (1976) and Grundy & Sutton (1989) explained the cohort-splitting in *Philoscia muscorum* by the fact that the late recruits had a smaller body size in winter, and were subject to greater retardation of growth resulting from cold. These authors also surmised that environmental cues were likely to synchronize breeding, with only two peaks of recruitment leading respectively to the two life cycles. In *P. angustus*, cohort-splitting mainly results from two mechanisms that we have identified and which can have effects even on individuals born on the same date:

(1) Individuals reaching the penultimate stadium (stadium VII) towards the end of spring have their final moult blocked and delayed for several months. As a result, practically no adults are produced from mid-July until mid-September. This aestivation only involves stadium VII, all other immature stadia moulting throughout the summer. It is usually late recruits from the previous year that enter aestivation, but the results obtained with a mild winter show that the hatching date is not the deciding factor. In fact, all the individuals that reach stadium VII after a critical period (early June for males and late June for females in our cultures) enter aestivation, irrespective of their hatching date.

(2) Adult females emerging in early autumn never breed before winter. Provided an adult male is present, mating takes place immediately after emergence, as in other polydesmid species (Stephenson, 1961; Snider,

1981b), but no eggs are laid between October and March, this being a sign of reproductive dormancy at this period.

Aestivation in subadults combined with reproductive dormancy in autumn-maturing females is the basis of cohort-splitting in *P. angustus*. The proportions of the two life cycles within a cohort seem to depend entirely on the proportions of individuals that reach stadium VII before and after the start of aestivation. For a given period of entry to aestivation (in June in our cultures), these proportions depend firstly on the birthday of individuals; the earlier this is the more chance they have of reaching stadium VII before aestivation in the following year. The proportions of the two life cycles also vary in relation to all those environmental factors that influence the rate of post-embryonic development between birth and the period of entry to aestivation. The data in Fig. 3 show that winter temperatures play a major role, as does food quality which has been shown to affect the rate of development during this period of the year (David & Célérier, 1997). This may result in yearly fluctuations in the number of individuals following the two life cycles in a population, and this could explain variations in life-cycle duration among populations in relation to their geographical or ecological situations.

Furthermore, the period of entry to aestivation may also vary in relation to environmental factors. This depends on the physiological mechanism that blocks the final moult in *P. angustus*. The data in Fig. 2 suggest at least two different explanations: (1) the suddenness of the entry into aestivation in June, that occurs at almost the same time at Brunoy and in Montpellier, suggests an effect of the increase in temperature from June onwards (mean 16°C; maximum 18°C); (2) on the other hand, the progressive decrease in the length of aestivation for subadults emerging in July and August, when temperature is higher than in June (mean 18°C; maximum 20°C), suggests an effect of photoperiod – aestivation length decreasing with daylength as in certain insects (Košťál & Hodek, 1997). A possible hypothesis is that the aestivation in stadium VII is a diapause induced by the increase in daylength during spring, but with a threshold temperature for photoperiodic response that is only reached in June. We are currently working on this hypothesis.

Similarly, the reproductive dormancy of autumn-maturing females may be a diapause induced by photoperiod. The absence of any egg laying during the autumn was probably not due just to the decrease in temperature in our cultures. Females maturing in early May (mean temperature 13°C) were capable of completing their first nest less than four weeks later, whereas no female maturing in late September-early October laid eggs in October, when temperature was almost the same as in May (mean 12°C). The possibility of an adult diapause induced by the decrease in daylength, as in woodlice (Souty-Grosset et al., 1994), is worthy of further investigations. In the only experimental study of periods of dormancy in a millipede, Fujiyama & Yoshida (1984) showed that adults of *Parafontaria laminata armigera* Verhoeff (Polydesmida: Xystodesmidae) collected in early autumn were in

reproductive dormancy and that a long period of chilling was needed for eggs to be laid. This led Fujiyama (1996) to suggest that temperature is the most important factor in regulating the life cycle of soil arthropods. Nevertheless, the induction of reproductive dormancy has not been investigated in *P. laminata armigera* and it may be related to photoperiodic conditions in late summer.

Although life-cycle regulation by photoperiod has never been demonstrated in a millipede (Hopkin & Read, 1992), this cannot be excluded, especially in a species such as *P. angustus* that lives more in leaf litter and logs than deep in the soil. The fact that the Polydesmida are blind is not a problem since sensitivity to light has been demonstrated in several species belonging to this order (Cloudsley-Thompson, 1951; Bellairs et al., 1983). The presence of photoreceptors on the 7th antennal segment of polydesmids was suggested by Fuhrmann (1922), and it is known that extraretinal photoreceptors are sensitive to photoperiod in other arthropods (Numata et al., 1997). An effect of photoperiod on the aestivation in subadults and the reproductive dormancy in females of *P. angustus* is therefore entirely plausible, and there is a pressing need for laboratory studies on this point.

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